



## Final Scientific Report

### Cover Page

**BARD Project Number: : IS-4179-08-R**

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**Project Title: Study of the physiological, molecular and genetic factors associated with post postharvest water loss in pepper fruit**

#### Investigators

**Principal Investigator (PI):** Elazar Fallik

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**Collaborating Investigators:** Ilan Paran

#### Institutions

ARO-the Volcani Center

Purdue University

ARO-the Volcani Center

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**Keywords** *not* appearing in the title and in order of importance. Avoid abbreviations.  
Back cross; *Capsicum annuum* L; *Capsicum chinense*; Cuticle; Quantitative trait loci

**Abbreviations commonly** used in the report, in alphabetical order: Back cross – BC;  
Quantitative trait loci – QTL; Water loss (WL)

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Signature  
Principal Investigator

Signature  
Authorizing Official, Principal Institution



## Final Scientific Report

### Publication Summary (numbers)

	Joint IS/US authorship	US Authors only	Israeli Authors only	Total
Refereed (published, in press, accepted) BARD support acknowledged	1			1
Submitted, in review, in preparation*	1			1
Invited review papers				
Book chapters	1			1
Books				
Master theses				
Ph.D. theses	1		1	2
Abstracts	2			2
Not refereed (proceedings, reports, etc.)	2			2

\*possible another paper will be submitted.

**Postdoctoral Training:** List the names and social security/identity numbers of all postdocs who received more than 50% of their funding by the grant.

### Cooperation Summary (numbers)

	From US to Israel	From Israel to US	Together, elsewhere	Total
Short Visits & Meetings	1	1		2
Longer Visits (Sabbaticals)				

### Description Cooperation:

The seeds of the two parental lines and selected BC2 and BC2F2 families were sent to Dr. Matthew Jenks at Purdue University where his lab grew the plants in a greenhouse for fruit cuticle lipid analysis. A short visit of E. Fallik was made to M. Jenks' lab to discuss the F2, BC2 and BC2F2 families' structure scheme and the first results that were obtained for fruit water loss. Jenks visited the Israeli team at the end of the first year research to discuss the latest information the US and the Israeli teams have obtained. Work is underway to link the QTL markers with specific variation in cuticle lipid composition, with preliminary results indicating some correlation between fruit water loss, cuticle free fatty acids and iso-alkanes, and new QTL markers (2 on chromosome 10). Studies to validate these linkages are underway now.

### Patent Summary (numbers)

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Submitted				
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## Final Scientific Report

### Summary

The fruit of pepper (*Capsicum annuum*) commonly wilts (or shrivels) during postharvest storage due to rapid water loss, a condition that greatly reduces its shelf life and market value. The fact that pepper fruit are hollow, and thus have limited water content, only exacerbates this problem in pepper. The collaborators on this project completed research whose findings provided new insight into the genetic, physiological, and biochemical basis for water loss from the fruits of pepper (*Capsicum annuum* and related *Capsicum* species). Well-defined genetic populations of pepper were used in this study, the first being a series of backcross F<sub>1</sub> and segregating F<sub>2</sub>, F<sub>3</sub>, and F<sub>4</sub> populations derived from two original parents selected for having dramatic differences in fruit water loss rate (very high and very low water loss). The secondly population utilized in these studies was a collection of 50 accessions representing world diversity in both species and cultivar types. We found that an unexpectedly large amount of variation was present in both fruit wax and cutin composition in these collections. In addition, our studies revealed significant correlations between the chemical composition of both the fruit cuticular waxes and cutin monomers with fruit water loss rate. Among the most significant were that high alkane content in fruit waxes conferred low fruit water loss rates and low permeability in fruit cuticles. In contrast, high amounts of terpenoids (plus steroidal compounds) were associated with very high fruit water loss and cuticle permeability. These results are consistent with our models that the simple straight chain alkanes pack closely together in the cuticle membrane and obstruct water diffusion, whereas lipids with more complex 3-dimensional structure (such as terpenoids) do not pack so closely, and thus increase the diffusion pathways. The backcross segregating populations were used to map quantitative trait loci (QTLs) associated with water loss (using DART markers, Diversity Arrays Technology LTD). These studies resulted in identification of two linked QTLs on pepper's chromosome 10. Although the exact genetic or physiological basis for these QTLs function in water loss is unknown, the genotypic contribution in studies of near-isogenic lines selected from these backcross populations reveals a strong association between certain wax compounds, the free fatty acids and iso-alkanes. There was also a lesser association between the water loss QTLs with both fruit firmness and total soluble sugars. Results of these analyses have revealed especially strong genetic linkages between fruit water loss, cuticle composition, and two QTLs on chromosome 10. These findings lead us to further speculate that genes located at or near these QTLs have a strong influence on cuticle lipids that impact water loss rate (and possibly, whether directly or indirectly, other traits like fruit firmness and



## Final Scientific Report

sugar content). The QTL markers identified in these studies will be valuable in the breeding programs of scientists seeking to select for low water loss, long lasting fruits, of pepper, and likely the fruits of related commodities. Further work with these newly developed genetic resources should ultimately lead to the discovery of the genes controlling these fruit characteristics, allowing for the use of transgenic breeding approaches toward the improvement of fruit postharvest shelf life.

### Introduction and previous findings

During postharvest storage, pepper (*Capsicum annuum*) fruit commonly wilts (or shrivels) early because of rapid water loss combined with the hollow fruit's limited water storage capacity, a condition that greatly reduces its shelf life and market value. A normal water loss distribution (Gauss distribution) was observed in the BC2 populations, and which was obtained during the research's first year. The parental line 1154 (high water loss) had about a 60% higher water loss rate than the line USDA162 (low water loss). The F1 value indicates dominant control for low water loss. DNA was extracted from all the BC1 and BC2 individuals and sent to Diversity Arrays Technology LTD for genotyping the population with DART markers for QTL analysis. In addition, we genotyped the population with COSII markers, in order to anchor the DART-based map with previous pepper maps. We obtained DART data in December 2009 and constructed genetic maps of the BC1 and BC2 populations from a cross of *Capsicum chinense* USDA162 (low water loss parent) X *C. annuum* '1154' (high water loss parent). The map consists of 141 molecular markers distributed throughout the genome, and these have been used for early QTL analysis of water loss segregation in these populations. Three QTLs were identified; 2 QTLs on chromosome 10 and 1 QTL on chromosome 5. Each of the QTL explains about 10% ( $R^2$ ) of the phenotypic variation of the trait. A further population of BC2F2 was constructed, and selected BC2F2 individuals derived from the original BC2 population was used to determine their water loss and the amount of various lipid chemical constituents of the cuticle (2010-2011). Significant correlations were found between fruit water loss and content of terpenoids and sterols, and the wax components: alkanols, alkenols and iso-alkanes. Our finding indicate that high alkane content associates with low water loss by fruits, whereas high amounts of terpenoids and sterols are associated with high water loss by fruits. These results support to our current cuticle permeability models proposing that alkanes and related compounds (because they lack side group modifications) will pack together very closely in the cuticle creating highly crystalline regions that, when



## **Final Scientific Report**

abundant, cause cuticles to be much less permeable. By comparison, our model also hypothesizes that the terpenoids and sterols (having more complex 3-dimensional structure) will not pack closely in the cuticle and, when abundant in the cuticle, allow for more of the amorphous diffusion pathways and thus cause cuticle to be more permeable.

## **Results (2011-2012)**

### **Verification of QTLs controlling fruit water loss (FrWL) in BC3F3**

To verify the effect of the three QTLs detected in BC2, we performed subsequent QTL mapping in the following populations:

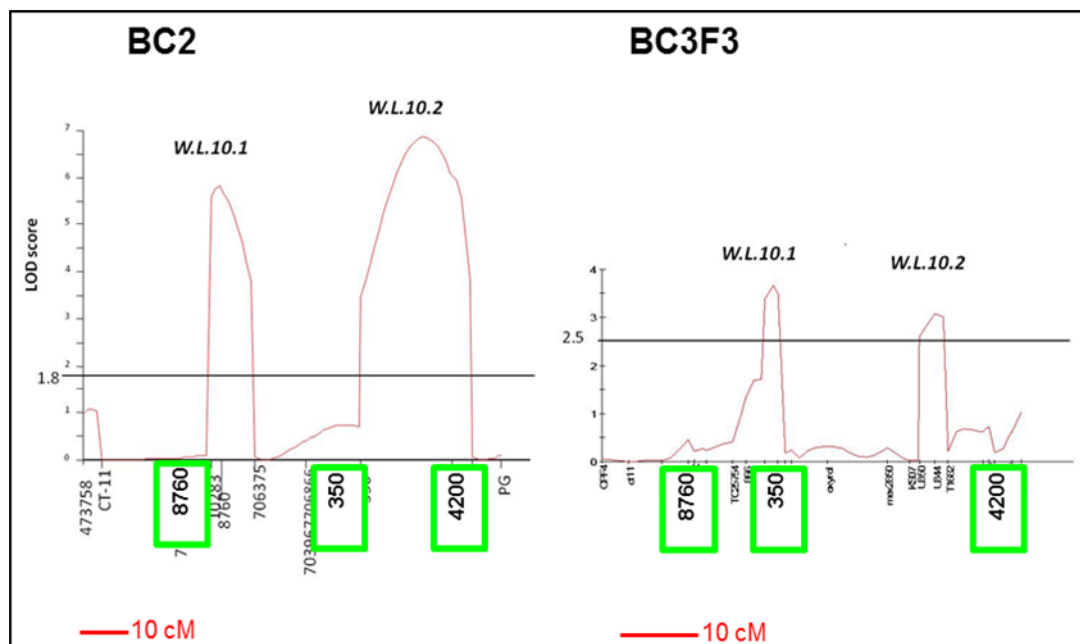
1. BC2F2 population (231 families) originated from selfing of BC2 plants. The population was grown in the open field and was sampled in summer 2009.
2. BC3 population derived from 30 BC2 plants exhibiting extreme water loss values. We generated 30 BC3 families: 15 from high water loss BC2 plants and 15 from low water loss BC2 plants. The population was planted in the greenhouse and was sampled in winter 2010-11.
3. BC3F3 population was generated from a single BC3F2 plant heterozygous for the 3 QTLs. 164 plants from this population were grown in a net-house and sampled in summer 2011. Enrichment of the introgression region in chromosome 10 with additional markers allowed refining the map position of the QTLs locations (Figure 1).

The QTL mapping data from the different populations are summarized in Table 1. Because we could not verify the effect of the QTL in chromosome 5 (W.L 5.1), we further focused on the 2 QTLs in chromosome 10 (Table 1).



## Final Scientific Report

**Figure 1.** QTL mapping of FrWL in BC2 and BC3F2



**Table 1.** Summary of QTLs in the different mapping populations

QTL	Marker	BC2				BC2F2		BC3		BC3F3	
		Aa <sup>1</sup>	aa <sup>1</sup>	R <sup>2</sup>	P	R <sup>2</sup>	P	Selected families		R <sup>2</sup>	P
W.L 5.1	DaRT 457280	19.6	21.9	0.077	0.0001**	Not significant		0.49	0.001*	0.021	0.2
W.L 10.2	COSII 01350	18.5	21.8	0.131	0.0001**	0.1	0.0001**	0.37	0.0007*	0.253	0.0001**
W.L 10.2	COSII 04200	18.5	21.6	0.097	0.0001	0.0003	0.8	0.04	0.3	0.148	0.0001**
W.L 10.1	COSII 08760	19.4	22	0.1	0.0001**	0.1	0.0001**	0.51	0.0002*	0.0869	0.0017

\* =  $P \leq 0.001$

\*\* =  $P \leq 0.0001$



## Final Scientific Report

### Generation and characterization of QTL-NILs

To further fine map and characterize the QTLs we constructed near-isogenic BC3F4 lines for the QTL in chromosome 10 (QTL-NIL).

Physiological measurements of fruit ripening traits were taken from all NILs. A t-test between each pair of NILs was performed to evaluate the effect of the QTL alleles on the physiological traits (Table 2). The NILs differed significantly for FrWL ( $P < 0.0001$ ).

NILs genotype explains 62% and 54% of FrWL variance in red and green fruit, respectively. As expected, the low FrWL values were associated with the introgression of the donor parent. The occurrence of a significant effect of FrWL already in the green unripe fruit indicated that FrWL is at least partly determined prior to fruit ripening.

NILs genotype explains more than 15% of fruit firmness variation before and after storage, and 25% of total soluble solids (TSS) variation before storage. Observing the differences between NILs in fruit firmness and TSS before storage indicate that FrWL is at least partly associated with firmness and TSS prior to fruit harvest.

**Table 2.** Physiological measurements of FrWL QTL-NILs.

	Mean value		$R^2$	P
	High WL NILS	Low WL NILS		
Red fruit water loss (mg/cm <sup>2</sup> )	40	21.6	0.62	0.0001
Green fruit water loss (mg/cm <sup>2</sup> )	33.4	19.1	0.54	0.0028
Firmness before storage (mm/cm <sup>2</sup> )	10.86	7.98	0.17	0.008
Firmness after storage (mm/cm <sup>2</sup> )	13.69	8.364	0.16	0.0005
TSS before storage (%)	10.38	9.46	0.25	0.0009
TSS after storage (%)	12.3	11.9	Not significant	



## Final Scientific Report

### Metabolic analyses of the QTL-NILs

Wax components measurements (a total of 10 components) were taken from two NILs. t-test between the NILs was performed to study the genetic effect on wax components (Table 3). NIL genotype explains 69% of the variation of wax-cuticle free fatty acids content. High free fatty acids content was associated with the presence of the recurrent parent genotype (high FrWL). NIL genotype explains 55% of the variation of wax-cuticle Iso alkanes content. High Iso alkanes content was associated with the presence of the donor parent genotype (low FrWL). Total wax content was not significantly associated with FrWL variation.

**Table 3.** Significant metabolic components between FrWL QTL-NILs.

Wax Components ( $\mu\text{g}/\text{dm}^2$ )	Mean value		$R^2$	P
	High	Low		
	WL NIL	WL NIL		
Free fatty Acids	42.77	25	0.69	0.0026
Iso alkanes	1.75	3.49	0.55	0.014
<b>Total</b>	<b>211</b>	<b>238</b>	<b>0.09</b>	<b>0.38</b>

### Water loss values of pepper accessions.

The results of the metabolic analyses of FrWL QTL-NILs were supported by a wider survey of 23 diverse pepper genotypes from a world-wide collection for which FrWL and cuticle composition were measured. FrWL measurements were correlated with cutin and wax components in all lines. Free fatty content acid was one of several components that exhibited significant correlation with FrWL. Total wax contents was not significantly correlated with FrWL (Table 4).





## Final Scientific Report

**Table 4.** Correlations between FrWS and free fatty acids and total wax content in 23 pepper lines.

High resolution mapping of chromosome 10.	Wax components			QTLs controlling FrWL in
		r	P	
	Free fatty Acids	0.51	0.002	
	<b>Total</b>	<b>0.07</b>	<b>0.2</b>	

Previous mapping results indicated the occurrence of 2 linked QTLs in chromosome 10. The QTL-NILs were developed such that the donor introgression contains both QTLs. Therefore, we set out to separate the effect of both QTLs in different sub-NILs and to fine map the QTLs. NIL-F2 population was generated by crossing one pair of NILs. Approximately 600 F2 plants were screened for markers that flank the introgression and 250 recombinant plants were selected and planted in the greenhouse in Fall 2012. The increased recombination within the introgression and marker enrichment by transcriptome analysis (see below) will allow higher resolution mapping of the QTLs.

### Transcriptome analysis

Fruit's RNA from one pair of NILs was sent (November 2012) to transcriptome sequence analysis (RNA-seq). The RNA was extracted from pericarp of fruits at 3 developmental stages-1 (young), 4 (mature green) and 6 (ripe) weeks-after anthesis. Differential expression analysis will reveal potential candidates for controlling FrWL in pepper. Furthermore, sequence comparison between NILs will allow identification of single nucleotide polymorphisms (SNPs) for marker enrichment of the QTL regions.

### Correlation between cuticle composition and water loss

To understand the role of fruit cuticle lipid composition in fruit water loss, an advanced back-cross population, the BC<sub>2</sub>F<sub>2</sub>, was created between the *C. annuum* (PI1154) and the *C.*



## Final Scientific Report

*chinense* (USDA162) which have high and low postharvest water loss rates respectively. Besides dramatic differences in fruit water loss, preliminary studies also revealed that these parents exhibited significant differences in both the amount and composition of their fruit cuticle. Cuticle analysis of the BC<sub>2</sub>F<sub>2</sub> fruit revealed that although water loss rate was not strongly associated with the total wax amount, there were significant correlations between water loss rate and cuticle composition (Table 5). We found a positive correlation between water loss rate and the amount of total triterpenoid plus sterol compounds, and negative correlations between water loss and the alkane to triterpenoid plus sterol ratio (Table 6). We also report negative correlations between water loss rate and the proportion of both alkanes and aliphatics to total wax amount. In cutin we found positive associations of water loss rate with total cutin, total C<sub>16</sub> monomers and with the 16-dihydroxy hexadecanoic acid (data not shown). As it relates to waxes, our findings indicate that high alkane content associates with low water loss by fruits, whereas high amounts of terpenoids and sterols are associated with high water loss by fruits. These results support to our cuticle permeability models proposing that alkanes and related compounds (because they lack side group modifications) will pack together very closely in the cuticle creating highly crystalline regions that, when abundant, cause cuticles to be much less permeable. By comparison, our model also hypothesizes that the terpenoids and sterols (having more complex 3-dimensional structure) will not pack closely in the cuticle and, when abundant in the cuticle, allow for more of the amorphous diffusion pathways and thus cause cuticle to be more permeable. The findings here shed new light on the role of cuticle chemical constituents in fruit water loss, on the inheritance of fruit cuticle traits, and lays the groundwork for ongoing studies to identify specific quantitative trait loci (QTLs) that can be used for the genetic improvement of fruit shelf-life in pepper.



## Final Scientific Report

**Table 5.** Cuticular wax composition of red-ripe pepper fruit cuticle extracted from 20 selected BC<sub>2</sub>F<sub>2</sub> plants and parental lines. Total wax amounts were expressed as  $\mu\text{g}/\text{dm}^2$  of fruit surface area  $\pm$  s.e. (n=3). Individual wax classes are expressed as percentages of the total amount. Free fatty acids (Acids), aldehydes, 1-alcohols (1-Alkanols.), *n*-alkanes, *iso*-alkanes, *anteiso*-alkanes, triterpenoids and sterols.

Accession	Wax amount	Acids	Aldehydes	1-Alkanols	Alkenols	Alkenes	<i>n</i> -Alkanes	<i>iso</i> -Alkanes	<i>anteiso</i> -Alkanes	Terpenoids /Sterols
USDA162	215 $\pm$ 14	14.5	5.4	7.6	0.5	2.1	47.4	6.2	1.6	14.6
16	218 $\pm$ 11	16.6	2.7	6.3	0.0	4.5	34.6	0.2	0.2	35.0
14	306 $\pm$ 29	10.1	4.7	9.4	0.0	2.1	13.9	0.9	0.5	71.9
12	324*	4.4	1.8	18.9	0.0	1.3	15.4	1.7	1.1	47.7
11	335 $\pm$ 4	15.3	2.1	7.9	0.0	11.9	22.4	1.5	0.5	36.2
9	393*	21.5	3.0	8.6	0.0	4.4	24.8	1.6	0.6	31.6
4	412 $\pm$ 21	8.9	2.5	6.5	0.3	5.2	36.4	3.2	1.3	36.0
8	438 $\pm$ 11	6.0	0.9	7.1	0.0	4.1	22.0	1.3	0.4	58.1
20	439 $\pm$ 27	22.1	1.8	7.0	0.0	3.9	29.4	0.7	1.0	38.0
13	441 $\pm$ 36	14.1	2.7	8.7	1.5	0.7	28.1	2.1	0.6	38.0
5	456 $\pm$ 84	7.7	5.1	9.8	0.4	2.1	34.9	2.3	2.3	43.2
10	472 $\pm$ 36	18.2	2.2	6.1	0.6	5.8	32.3	1.7	0.8	33.0
6	497 $\pm$ 25	17.6	3.0	7.1	0.0	0.7	26.1	1.2	1.6	37.5
18	497 $\pm$ 34	15.4	3.2	7.6	0.0	7.3	26.3	2.6	0.5	37.6
1	531 $\pm$ 16	16.2	4.4	7.5	0.8	4.6	36.7	2.5	1.3	26.4
19	552 $\pm$ 77	15.9	1.4	6.9	0.0	19.5	1.4	1.5	0.2	46.5
15	631 $\pm$ 30	16.3	3.2	6.2	0.0	4.4	14.1	0.2	4.1	53.1
2	632 $\pm$ 42	5.9	2.6	8.0	0.0	2.6	27.2	0.4	0.2	30.5
PI 1154	634 $\pm$ 39	4.6	0.8	6.7	0.1	1.1	11.6	1.4	0.4	73.3
3	663 $\pm$ 34	8.5	2.7	6.2	0.2	6.5	28.4	2.2	0.8	36.1
7	749 $\pm$ 37	5.4	1.4	7.1	0.0	1.3	35.9	1.0	0.9	42.1
17	752 $\pm$ 64	16.5	2.9	8.7	1.3	5.3	27.5	3.5	0.4	34.4

Standard errors for the wax classes in this table were not shown, but are comparable in proportions to deviations of the total wax amounts shown. \* n=1.

**Table 6.** Correlation coefficients of water loss rate and total amount of each wax class from selected BC<sub>2</sub>F<sub>2</sub> plants. Classes include *n*-alkanes, *iso*-alkanes, triterpenoids and sterols (T & S). Total alkanes include *n*-alkanes, *iso*-alkanes and *anteiso*-alkanes; aliphatics include total alkanes plus aldehydes; Alp/T&S is the ratio of aliphatics to triterpenoids and sterols; Alk/T&S is the ratio of total alkanes to triterpenoids and sterols. p-value determined by student's t-test (n=14).

	Total amount	<i>n</i> -Alkanes	<i>iso</i> -Alkanes	Total Alkanes	Total Aliphatics	T & S	Alk/T&S	Alp/T&S
r	0.06	-0.67	-0.55	-0.51	-0.49	0.70	-0.71	-0.70
p- value	0.4	0.0025	0.025	0.05	0.05	0.0025	0.0025	0.0025



## Final Scientific Report

### Fruit cuticle lipid composition and water loss in a diverse collection of pepper (*Capsicum*)

Recent studies report that pepper fruit cuticle varies among commercial cultivars, and that this variation likely influences fruit quality traits, especially post-harvest water loss (Riederer and Schrieber 2001, Maalekuu et al. 2003). However, previous studies have been limited to just a few pepper genotypes (Riederer and Schrieber 2001, Maalekuu et al. 2003). To shed light on the chemical-compositional diversity of cuticles in pepper, the fruit cuticles from 50 diverse pepper genotypes from a world collection were screened for both wax and cutin monomer amount and composition. These same genotypes were also screened for fruit water loss rate and this tested for associations with cuticle composition. Our results revealed an unexpectedly large amount of variation for the fruit cuticle lipids, with a more than fifteen-fold range for total wax amount and a more than sixteen-fold range for cutin monomer amount between the most extreme accessions. Within the major wax constituents fatty acids varied from 1 to 45%, primary alcohols from 2 to 21%, *n*-alkanes from 9 to 73% and triterpenoids and sterols from 10 to 75%. Within the cutin monomers, total hexadecanoic acids ranged from 54 to 87%, total octadecanoic acids ranged from 10 to 38%, and coumaric acids ranged from 0.2 to 8% of the total cutin. We also observed considerable differences in water loss among the accessions, and unique correlations between water loss and cuticle constituents. The water loss assay revealed approximately 8-fold difference between the highest and lowest value. We report significant negative correlations between *n*-alkane proportions and water loss, as well as the ratio of *n*-alkanes to triterpenoid plus sterols (similar as in our BC2 population studies reported above), confirming that these wax chemical compositions are determinants of fruit water loss. Correlations with cutin composition and water loss rates were not as strong in this study as they were in the BC2 population study above, likely because this was a much more diverse population and other factors, whether cuticular and/or non-cuticular, may play an important role in fruit water loss. The resources described here will be valuable for future studies of the physiological function of fruit cuticle, for the identification of genes and QTLs associated with fruit cuticle synthesis in pepper fruit, and as a starting point for breeding improved fruit quality in pepper.



## Final Scientific Report

### Appendix

**Table 1.** Accessions used in this study. The table includes accession numbers, species, cultivar/trade name, origin, and codes used in subsequent tables.

Accession	Species	Cultivar /Tradename/Plantid	Origin	Code #
08C608	<i>Capsicum annuum</i>		New Mexico	1
08C609	<i>Capsicum annuum</i>		New Mexico	2
08C610	<i>Capsicum annuum</i>		New Mexico	3
08C611	<i>Capsicum annuum</i>		New Mexico	4
08C829	<i>Capsicum annuum</i>		New Mexico	5
09C374	<i>Capsicum annuum</i>		New Mexico	6
09C375	<i>Capsicum annuum</i>	NuMex Las Cruces Cayenne	New Mexico	7
09C392	<i>Capsicum annuum</i>		New Mexico	8
09C395	<i>Capsicum annuum</i>		New Mexico	9
09C426	<i>Capsicum annuum</i>	Carolina Cayenne	New Mexico	10
PI 357531 <sup>#</sup>	<i>Capsicum annuum</i>	Recica Babura	Serbia/Montenegro	11
09C434	<i>Capsicum annuum</i>	Cascabel	New Mexico	12
09C520	<i>Capsicum annuum</i>		New Mexico	13
09C624	<i>Capsicum annuum</i>	Grande Jalapeno	New Mexico	14
09C773	<i>Capsicum annuum</i>	Ixtapa Jalapeno	New Mexico	15
09C978	<i>Capsicum annuum</i>	Marconi Red	New Mexico	16
Grif 9094 <sup>#</sup>	<i>Capsicum annuum</i>	GRC-GGB-4488	Greece	17
PI 785 <sup>#</sup>	<i>Capsicum annuum</i>		Israel	18
PI 339001 <sup>#</sup>	<i>Capsicum annuum</i>	Sweet Bell Pepper	Turkey	19
PI 357539 <sup>#</sup>	<i>Capsicum annuum</i>	Belozolta Babura	Serbia/Montenegro	20
PI 357576 <sup>#</sup>	<i>Capsicum annuum</i>	Vezena Slatka	Serbia/Montenegro	21
PI 224421 <sup>#</sup>	<i>Capsicum annuum</i>	No.1582	Nicaragua	22
PI 379211 <sup>#</sup>	<i>Capsicum annuum</i>	Vezena Sr Ljuta	Serbia/Montenegro	23
PI 368066 <sup>#</sup>	<i>Capsicum annuum</i>		China, Hong Kong	24
PI 385960 <sup>#</sup>	<i>Capsicum annuum</i>	Jet-Set	Kenya	25
PI 432802 <sup>#</sup>	<i>Capsicum annuum</i>	Qie Men 30	China	26
PI 586669 <sup>#</sup>	<i>Capsicum annuum</i>	Wonder Giant	California	27
PI 592825 <sup>#</sup>	<i>Capsicum annuum</i>	King Of The North	Michigan	28
PI 592831 <sup>#</sup>	<i>Capsicum annuum</i>	Sweet Chocolate	Michigan	29
PI 592834 <sup>#</sup>	<i>Capsicum annuum</i>	Titan	California	30
PI 631126 <sup>#</sup>	<i>Capsicum annuum</i>	Grif 974	China, Beijing	31
09C270	<i>Capsicum baccatum</i> *	Christmas Bell	South America	32
09C271	<i>Capsicum baccatum</i>	Escabeche	Bolivia	33
09C272	<i>Capsicum baccatum</i>	NMCA 20064	New Mexico	34
09C274	<i>Capsicum baccatum</i>	Pucomucho	Peru	35
09C278	<i>Capsicum baccatum</i> *	Omnicolor	Peru	36
09C261	<i>Capsicum chinense</i>	Habanero	New Mexico	37
09C322	<i>Capsicum chinense</i>	Caribbean Red Habanero	Mexico	38
Grif 9325 <sup>#</sup>	<i>Capsicum frutescens</i>	Peru-5411	Costa Rica	39
Grif 9327 <sup>#</sup>	<i>Capsicum frutescens</i>	Peru-5490	Costa Rica	40
PI 195299 <sup>#</sup>	<i>Capsicum frutescens</i>	2645	Guatemala	41
PI 370007 <sup>#</sup>	<i>Capsicum frutescens</i>		India	42
PI 585276 <sup>#</sup>	<i>Capsicum pubescens</i>	Ecu 6225	Ecuador, Napo	43
PI 593621 <sup>#</sup>	<i>Capsicum pubescens</i>	80038	Guatemala	44
PI 257104 <sup>#</sup>	<i>Capsicum spp.</i>	ISCA	Colombia	45
PI 257046 <sup>#</sup>	<i>Capsicum spp.</i>	Aji Dulce	Colombia	46
PI 439450 <sup>#</sup>	<i>Capsicum spp.</i>	2102	Peru	47
Leros Long <sup>#</sup>	<i>Capsicum annuum</i>		Greece, Leros	48
Leros Round 1 <sup>#</sup>	<i>Capsicum annuum</i>		Greece, Leros	49
Leros Round 2 <sup>#</sup>	<i>Capsicum annuum</i>		Greece, Leros	50

\* *var. pendulum*

<sup>#</sup> Indicates greenhouse grown peppers, all others were field grown



## Final Scientific Report

**Table 2.** Cuticular wax composition of pepper fruit extracted from selected Capsicum accessions. Wax amounts were expressed as  $\mu\text{g}/\text{dm}^2$  of fruit surface area  $\pm$  s.e. ( $n=3$ ). Individual wax classes include: free fatty acids (Acids), aldehydes, 1-alcohols (1-Alc.), di/trienols (Di/Tri.), alkenes, n-alkanes, iso-alkanes (i-Alkanes), anteiso-alkanes (a-Alkanes), triterpenoids and sterols (T&St).

Code #	Total	Acids	Aldehydes	1-Alc.	Di/Tri	Alkenes	n-Alkanes	i-Alkanes	a-Alkanes	T&S
26	95.5 $\pm$ 5.8	26.1	3.9	4.9	0.0	1.8	31.4	3.0	0.6	22.9
19	97.0 $\pm$ 14.8	18.5	1.6	3.8	0.0	8.2	22.6	2.4	1.1	38.8
25	112.5 $\pm$ 12.9	22.4	3.6	11.7	0.0	3.6	45.8	4.2	2.2	29.4
39	131.5 $\pm$ 11.7	47.0	3.3	6.3	0.0	1.2	50.3	3.4	0.9	19.2
10	217.1 $\pm$ 63.0	57.4	10.9	14.4	6.6	1.8	62.9	3.5	1.3	107.5
33	221.1 $\pm$ 13.1	66.5	8.5	18.6	14.6	30.3	46.9	1.0	0.9	34.9
14	263.0 $\pm$ 20.4	18.9	3.3	19.0	8.4	2.0	107.4	6.8	0.3	97.1
35	284.4 $\pm$ 57.4	1.9	0.0	25.7	0.0	0.0	182.6	5.3	2.7	27.6
2	339.2 $\pm$ 91.3	43.0	9.2	31.1	20.5	3.3	114.0	7.7	0.6	<b>73.9</b>
6	348.7 $\pm$ 9.4	63.2	10.0	62.6	41.5	8.4	82.6	4.3	1.5	94.3
15	380.3 $\pm$ 25.1	42.9	8.7	27.2	11.1	2.2	187.1	7.6	1.1	92.3
38	398.8 $\pm$ 11.1	19.9	8.4	10.0	34.5	1.7	291.2	6.4	0.7	42.8
45	418.0 $\pm$ 17.9	74.5	3.3	24.7	0.0	0.0	168.6	0.0	2.8	116.6
1	421.5 $\pm$ 56.9	88.8	18.9	61.7	10.0	4.6	166.4	9.9	1.2	157.3
7	423.2 $\pm$ 36.3	107.7	7.4	7.5	0.0	7.2	101.9	12.5	2.8	136.1
41	428.3 $\pm$ 39.6	76.6	9.5	11.3	0.0	6.6	136.8	4.3	0.5	235.6
48	430.3 $\pm$ 14.5	42.4	7.2	19.4	0.0	39.9	191.8	19.5	5.0	112.6
4	434.4 $\pm$ 41.9	66.9	21.4	68.6	12.0	5.5	144.2	15.7	1.5	106.9
3	435.3 $\pm$ 22.2	88.5	16.3	55.2	14.4	6.3	144.8	9.6	0.7	91.4
36	452.0 $\pm$ 87.1	57.9	1.9	106.0	10.0	38.8	224.2	2.7	1.8	73.6
12	457.8 $\pm$ 72.1	62.0	5.5	40.1	17.9	5.6	73.8	5.4	0.2	235.0
40	472.0 $\pm$ 54.8	83.6	10.3	35.5	0.0	3.5	139.5	7.5	1.0	177.3
37	503.8 $\pm$ 127.7	33.3	14.1	73.7	31.6	3.5	292.0	5.2	3.2	62.4
46	518.3 $\pm$ 13.7	75.0	8.8	27.3	0.0	19.1	210.3	2.4	1.7	187.1
27	530.7 $\pm$ 55.2	94.9	3.5	43.4	0.0	48.6	150.5	12.0	6.1	124.3
5	533.3 $\pm$ 65.6	94.7	14.6	47.0	9.0	21.5	189.5	13.0	3.6	144.9
47	561.0 $\pm$ 14.4	252.2	5.9	26.6	0.0	2.6	175.9	12.4	4.9	80.5
8	564.2 $\pm$ 5.3	67.5	20.0	66.7	45.7	3.4	281.6	9.8	1.3	86.9
42	565.1 $\pm$ 54.4	34.7	6.1	38.6	0.0	16.1	196.7	24.5	3.2	263.4
11	575.8 $\pm$ 10.6	90.7	10.6	36.8	4.0	37.4	132.3	23.4	3.7	236.9
30	582.2 $\pm$ 15.0	125.6	17.3	28.9	0.0	29.8	183.4	23.9	5.7	167.6
24	603.8 $\pm$ 34.5	99.0	18.2	65.2	3.4	16.3	114.0	8.0	1.5	276.5
16	607.8 $\pm$ 40.0	72.0	9.2	35.8	5.2	10.1	282.5	26.1	3.6	159.2
43	619.7 $\pm$ 81.2	107.2	16.4	51.5	0.0	0.0	124.7	16.2	4.2	271.8
49	620.1 $\pm$ 20.2	67.3	7.9	37.7	0.0	29.7	174.7	17.0	6.8	256.5
31	641.6 $\pm$ 14.3	133.5	22.0	68.5	0.0	0.0	210.4	21.9	2.9	131.0
9	658.8 $\pm$ 18.4	140.1	23.8	67.5	39.0	6.3	187.3	11.8	0.5	200.5
50	666.5 $\pm$ 34.0	87.1	10.8	48.3	0.0	79.8	208.5	17.0	5.6	240.9
17	676.7 $\pm$ 70.3	117.6	32.5	57.6	0.0	40.6	161.7	20.5	5.8	240.4
44	686.0 $\pm$ 25.4	73.7	35.8	33.6	0.0	48.7	250.8	10.6	10.5	222.6
22	726.5 $\pm$ 12.9	186.9	30.7	68.8	0.0	26.4	146.3	11.5	2.0	255.4
20	758.8 $\pm$ 37.2	162.4	20.9	58.2	0.0	31.7	210.4	23.7	5.8	258.8
18	766.4 $\pm$ 37.8	159.3	36.1	44.2	8.8	12.3	217.9	10.2	3.1	283.3
28	791.6 $\pm$ 32.1	88.2	9.9	33.0	0.0	59.4	159.8	19.8	6.3	359.0
29	792.1 $\pm$ 58.7	98.1	19.6	34.5	0.0	26.9	268.8	23.7	10.9	282.7
21	807.8 $\pm$ 119.1	192.7	30.4	82.9	0.0	18.9	166.7	10.9	3.9	196.1
13	812.7 $\pm$ 34.9	115.1	24.9	96.8	77.2	4.5	361.6	12.9	3.6	153.0
32	929.9 $\pm$ 18.6	67.8	10.5	140.7	0.0	64.1	432.0	9.1	8.8	151.5
34	1093.7 $\pm$ 62.1	73.7	11.5	156.8	0.0	66.0	502.0	7.0	0.0	234.1
23	1480.6 $\pm$ 42.0	462.3	62.1	242.4	8.2	34.5	275.1	40.5	2.5	348.0

Standard deviations for the wax classes in this table are not shown, but were comparable in proportions to deviations of the total wax amounts shown.



## Final Scientific Report

**Table 3.** Cutin monomer composition of pepper fruit cuticle extracted from selected *Capsicum* accessions. Total monomer amounts were expressed as  $\mu\text{g}/\text{dm}^2$  of fruit surface area  $\pm$  s.e. ( $n=3$ ). Cutin monomers included  $\omega$ -hydroxy hexadecanoic acid ( $\text{C}_{16:0}$   $\omega$ -OH); 10,16-dihydroxy hexadecanoic ( $\text{C}_{16:0}$  di-OH); hexadecane-1,16-dicarboxylic acid ( $\text{C}_{16:0}$  diC); 18-hydroxy octadecanoic ( $\text{C}_{18:0}$   $\omega$ -OH); 18-hydroxy octadecenoic acid ( $\text{C}_{18:1}$   $\omega$ -OH); 9,18-dihydroxy octadecanoic acid ( $\text{C}_{18:0}$  di-OH); 9,10,18-trihydroxy octadecanoic acid ( $\text{C}_{18:0}$  tri-OH); 9,10-epoxy-octadecanoic acid (Ep  $\omega$ -OH); 9,10-epoxy-octadecenoic acid (Ep18:1); *p*- and *m*-coumaric acids (CA).

Code #	Total Cutin	$\text{C}_{16:0}$ $\omega$ -OH	$\text{C}_{16:0}$ di-OH	$\text{C}_{16:0}$ diC	$\text{C}_{18:0}$ $\omega$ -OH	$\text{C}_{18:1}$ $\omega$ -OH	$\text{C}_{18:0}$ di-OH	$\text{C}_{18:0}$ tri-OH	Ep $\omega$ -OH	Ep 18:1	CA
44	254.6 $\pm$ 44.0	7.2	153.9	1.9	25.1	7.7	1.0	22.0	12.1	3.7	19.9
16	357.6 $\pm$ 10.5	9.4	180.2	2.9	74.7	11.5	10.2	9.4	27.0	12.4	20.0
30	380.0 $\pm$ 13.5	10.0	263.7	7.2	0.0	10.2	5.6	27.9	28.3	7.2	20.0
15	404.7 $\pm$ 49.4	12.2	275.3	2.5	33.2	7.7	7.0	19.0	23.6	8.3	15.8
29	429.8 $\pm$ 1.6	13.1	294.8	4.4	28.1	15.6	4.3	18.3	27.1	5.2	19.7
43	469.2 $\pm$ 15.1	7.5	360.8	12.6	0.0	5.4	1.2	13.1	6.1	37.6	25.0
31	482.6 $\pm$ 41.6	15.9	333.3	4.1	0.0	9.4	11.7	36.2	35.0	5.8	31.3
42	612.6 $\pm$ 5.4	24.2	475.4	5.0	0.0	5.9	13.1	48.3	24.7	6.3	9.7
1	615.9 $\pm$ 38.8	16.9	392.4	6.0	0.0	11.7	8.0	40.1	57.4	8.2	14.4
26	638.0 $\pm$ 55.9	21.9	457.3	4.4	0.0	11.4	11.3	38.8	48.8	17.1	27.0
49	662.7 $\pm$ 63.1	17.9	445.1	2.9	0.0	12.7	10.9	55.9	46.0	10.8	24.1
14	669.7 $\pm$ 64.2	25.0	528.2	5.2	0.0	12.8	10.4	25.0	33.6	6.5	23.0
4	749.6 $\pm$ 40.8	26.2	561.9	7.3	0.0	13.6	11.8	55.3	34.6	19.7	16.3
46	755.0 $\pm$ 115.2	22.4	584.7	6.2	0.0	14.7	13.4	41.4	19.3	9.3	43.7
13	807.0 $\pm$ 34.8	22.9	547.8	6.2	43.0	14.2	14.5	49.5	54.5	11.4	43.2
18	834.5 $\pm$ 104.1	28.8	595.6	6.4	6.7	19.3	14.3	73.8	57.4	7.2	23.1
50	846.3 $\pm$ 54.5	26.7	630.2	4.5	0.0	13.8	14.3	63.4	57.8	11.9	23.8
37	873.0 $\pm$ 81.7	37.4	683.9	4.0	40.3	12.3	13.5	40.4	24.5	5.6	14.4
8	875.2 $\pm$ 51.3	23.0	545.8	5.2	113.0	14.4	13.6	51.5	52.3	11.0	45.4
2	882.2 $\pm$ 63.1	28.7	652.8	12.8	0.0	14.5	16.5	64.2	48.3	20.8	18.4
38	910.3 $\pm$ 73.8	29.6	745.7	3.0	0.0	18.8	10.5	60.0	27.6	7.5	7.7
3	916.0 $\pm$ 44.0	31.3	648.6	8.5	0.0	17.5	18.9	57.8	89.1	12.4	28.7
9	954.1 $\pm$ 28.3	24.1	554.2	5.8	152.5	17.1	12.8	60.0	74.0	11.9	41.7
11	1089.8 $\pm$ 15.2	37.2	778.5	7.8	0	17.1	18.2	60.4	117.7	19.1	33.8
25	1144.1 $\pm$ 47.8	29.7	805.7	9.8	0.0	33.8	26.9	77.4	81.1	18.0	71.8
19	1144.7 $\pm$ 45.0	41.8	834.5	6.8	0.0	25.5	26.4	96.6	69.8	13.7	35.1
28	1159.2 $\pm$ 60.4	30.6	817.1	5.4	0.0	21.1	27.2	106.5	98.1	17.6	35.6
36	1163.0 $\pm$ 74.5	45.9	885.0	14.0	0.0	10.6	20.5	59.3	73.3	18.9	35.5
47	1176.7 $\pm$ 173.5	35.1	966.7	5.6	0.0	37.0	20.1	57.2	35.5	9.1	10.4
27	1217.0 $\pm$ 54.8	43.0	835.7	13.7	0.0	43.1	25.1	91.8	101.1	16.3	47.2
35	1255.3 $\pm$ 54.2	61.7	1028.6	7.6	0.0	19.8	9.6	63.1	30.6	7.4	27.0
20	1266.1 $\pm$ 29.7	46.2	982.3	15.6	0.0	16.7	12.8	74.3	65.5	16.8	35.7
34	1267.0 $\pm$ 43.4	57.5	1002.9	5.6	0.0	30.7	13.3	46.7	62.2	9.3	38.8
23	1272.1 $\pm$ 26.9	37.5	797.4	15.9	120.3	18.9	10.1	87.7	118.6	20.3	45.2
6	1332.4 $\pm$ 24.7	45.6	988.3	11.0	0.0	17.2	28.0	81.2	89.3	16.0	55.8
24	1478.9 $\pm$ 43.0	59.7	806.7	15.3	424.5	21.6	12.9	65.6	23.6	7.9	41.2
45	1485.2 $\pm$ 154.8	34.7	1220.9	6.5	0.0	29.0	22.6	84.7	35.8	10.3	2.3
10	1535.7 $\pm$ 80.2	39.7	995.2	11.1	150.9	19.2	9.6	123.8	107.0	22.0	57.2
22	1550.9 $\pm$ 8.2	45.4	986.0	14.0	247.9	19.9	27.9	59.7	87.0	24.7	38.3
48	1558.9 $\pm$ 39.3	43.5	1167.7	6.9	0.0	22.8	23.0	128.7	113.3	21.5	31.5
17	1578.7 $\pm$ 92.9	52.9	1132.5	10.2	0.0	46.3	29.7	113.5	119.6	28.3	46.4
21	1621.4 $\pm$ 417.1	38.5	1029.6	16.2	173.7	19.7	27.4	90.4	117.9	29.0	70.3
40	1628.1 $\pm$ 31.0	46.5	1251.2	8.8	82.2	22.9	21.9	89.2	59.5	13.6	32.2
32	1737.9 $\pm$ 339.8	52.6	1387.6	8.9	0.0	10.4	14.0	77.3	105.5	16.8	52.3
39	1798.5 $\pm$ 131.5	54.6	1394.7	5.7	73.8	36.7	31.2	106.4	60.1	14.0	21.3
5	1838.2 $\pm$ 118.5	73.9	1450.5	27.6	0.0	21.3	25.8	104.8	75.4	15.3	41.3
7	1842.5 $\pm$ 83.4	39.3	1269.9	7.5	0.0	16.3	42.8	180.6	199.1	32.3	54.7
41	1877.1 $\pm$ 377.1	51.8	1496.5	16.9	0.0	33.8	34.9	94.2	60.4	14.5	74.1
33	3293.7 $\pm$ 183.1	107.4	2521.4	7.5	108.7	18.7	25.3	161.5	155.3	66.5	121.5
12	4104.3 $\pm$ 33.5	80.1	3319.3	49.8	49.1	24.9	91.2	179.5	101.5	41.3	167.7

Standard errors for individual cutin monomers in this table were not shown, but are comparable in proportions to deviations of the total cutin monomer amounts shown.





## Final Scientific Report

### Description of the cooperation

The seeds of the two parental lines and selected BC2 and BC2F2 families were sent to Dr. Matthew Jenks at Purdue University where his lab grew the plants in a greenhouse for fruit cuticle lipid analysis. A short visit of E. Fallik was made to M. Jenks' lab to discuss the F2, BC2 and BC2F2 families' structure scheme and the first results that were obtained for fruit water loss. Jenks visited the Israeli team at the end of the first year research to discuss the latest information the US and the Israeli teams have obtained. Work is underway to link the QTL markers with specific variation in cuticle lipid composition, with preliminary results indicating some correlation between fruit water loss, cuticle free fatty acids and iso-alkanes, and new QTL markers. Studies to validate these linkages are underway now.

### Publications resulting from this work:

Paran I, Fallik E (2011). Breeding for fruit quality in pepper (*Capsicum* spp.). In: Breeding for Fruit Quality. Wiley-Blackwell Publishing Inc., Jenks MA, Bebeli, PJ (eds). Oxford Press UK, pp. 307-322.

Parsons EP, Popovvsky S, Lohrey GT, Lü S, Alkalai-Tuviab S, Perzelanb Y, Paran I, Fallik E, Jenks MA (2012). Fruit cuticle lipid composition and fruit postharvest water-loss in an advanced backcross generation of pepper (*Capsicum* sp.). *Physiologia Plantarum* 146:15-25.

Parsons EP, Popovvsky S, Lohrey GT, Lü S, Alkalai-Tuvia S, Perzelan Y, Bosland P, Bebeli PJ, Paran I, Fallik, Jenks MA (2013). Fruit cuticle lipid composition and water loss in a diverse collection of pepper (*Capsicum*). *Physiologia Plantarum* (submitted).

Popovvsky S, Parsons EP Lohrey GT, Shiyu Lü, Alkalai-Tuvia S, Perzelan Y, Borovasky Y Fallik E, Jenks MA, Paran I. (2012). QTL mapping, physiological and biochemical analyses of postharvest water loss in pepper fruit. SOL 2012 The 9th Solanaceae Conference. Neuchâtel, Switzerland.

Popovvsky-Sarid S, Parsons EP, Alkalai-Tuvia S, Perzelan Y, Fallik E, Jenks MA, Paran I 2010. The physiological, molecular and genetic factors associated with postharvest water loss in pepper fruit. XXVIII International Horticultural Congress, Lisbon, Portugal (see poster below).





## Final Scientific Report



# The physiological, molecular and genetic factors associated with postharvest water loss in pepper fruit\*

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\*Research supported by the Binational Agricultural Research and Development (BARD/USA-ISRAEL)

### INTRODUCTION

Bell pepper (*Capsicum annuum* L.) is a commercially important vegetable crop in both US and Israel with much potential for increasing its market share. However, marketing is limited by the relatively short storability and shelf life of the fruit due to high water loss and decay development soon after harvest. Our research is aimed at exploring the genetic control and the biological basis for observed variation in postharvest fruit water loss (FrWL) in pepper. We identified the two parents 'PI 1154' (*C. annuum*) and 'USDA 162' (*C. chinense*) exhibiting high and low FrWL, respectively. Biochemical characterization of cuticle composition (cutin and wax) and histological analysis of fruits from the two parents revealed significant differences. Quantitative trait locus (QTL) mapping of FrWL in a BC2 population in a cross of the two parents was performed, and correlation of FrWL with cuticle components was determined.

Figure 1. Stains of pericarp and cuticle sections of the two parents 'PI 1154' (*C. annuum*, high FrWL) and 'USDA 162' (*C. chinense*, low FrWL)

**A-** Fruits of the two parental lines that differ in FrWL  
**B-** Stains of Sudan red for fats, oils, and waxes reveal thicker wax cuticle layer in fruit of 'PI 1154' than in 'USDA 162'. In the fruit of 'USDA 162', wax is penetrating deeper into the inner layers compared with 'PI 1154'.  
**C-** Safranin/fast-green stain indicated that fruit of 'USDA 162' has cuticle pegs that penetrate into the epidermis layer, while the fruit of 'PI 1154' lacks these structures. This staining also revealed smaller epidermis cells and larger parenchymatic cells in 'PI 1154' compared to 'USDA 162'.  
**D-** Cuticle auto fluorescence under UV light results with much intense fluorescence emission from the fruit of 'USDA-162' compared to 'PI 1154'.

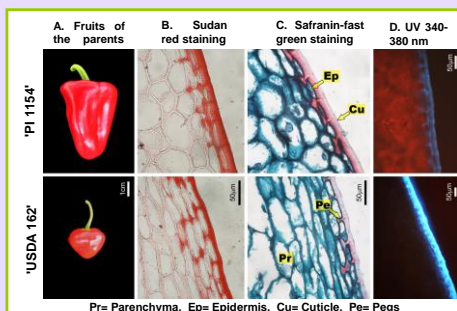


Figure 2. Water loss distribution in the BC2 population.

A normal distribution (Gauss distribution) was observed for FrWL in the BC2 population. Transgressive segregation was observed in the BC2 population. The parental line 'PI 1154' lost about 60% more water compared to 'USDA 162'.

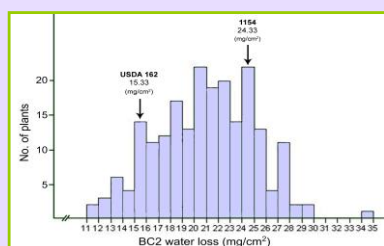
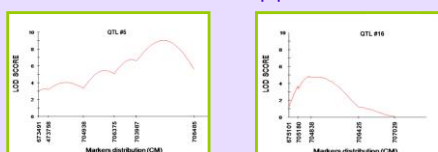


Figure 3. Quantitative trait loci (QTL) analysis for postharvest fruit water loss in the BC2 population



The BC2 population was genotyped with DaRT DNA markers covering an estimated 75% of the pepper genome. Based on anchoring the map with known COSII markers ([www.sgn.cornell.edu](http://www.sgn.cornell.edu)), two QTLs were identified in chromosomes 5 and 9.

### Summary

- Differences in cuticle structure and composition were found between the parents of the mapping population
- Two QTLs controlling fruit water loss were identified
- Significant correlations between fruit water loss and cuticle components were found
- Specific cutin and wax components but not total cutin and wax may account for variation in fruit water loss in pepper

Table 1. Water loss and composition of fruit cuticle of the parents

	'USDA 162' Mean ± SE	'PI 1154' Mean ± SE	USDA162 / PI 1154
Water Loss after 5 days (mg/cm²)	52.4 ± 0.1	116.5 ± 1.4	0.4
Fatty Acids	31.3 ± 3.0	54.6 ± 14.1	0.6
Terpenoids/Sterols	31.4 ± 2.8	409.3 ± 10	0.1
Alkanols	16.4 ± 1.8	42.4 ± 1.3	0.4
Alkenols	1.1 ± 0.2	3.6 ± 0.04	0.3
Total wax (ug/dm²)	215.4 ± 14.1	632.4 ± 16.1	0.3
16 diol	3.4 ± 0.9	11.4 ± 0.3	0.3
18-OH 18:0	260.9 ± 16.4	50.8 ± 27.3	5.1
9,18di-OH	6.3 ± 0.7	19.9 ± 0.7	0.3
epoxyw-OH	21.1 ± 2.2	94.5 ± 5.2	0.2
18:1 epoxy	6.6 ± 0.5	19.6 ± 5.3	0.3
Total cutin (mg/cm²)	764.3 ± 55.3	1196.7 ± 1.8	0.6

In general, the high FrWL parent 'PI 1154' had higher content of cuticle components than the low FrWL parent, with one exception of the cutin monomer 18-OH 18:0 which was 5-fold higher in 'USDA 162' than in 'PI 1154'. These results are in agreement with the thicker cuticle of 'PI 1154' shown in Figure 1.

Table 2. Cuticle composition in selected BC2F2 individuals and correlation with fruit water loss.

Plant No	Water Loss after 5 days (mg/cm²)	Total wax (ug/dm²)	Alkanols (ug/dm²)	Alkenols (ug/dm²)	iso-alkanes (ug/dm²)	Terpenoids and Sterols (ug/dm²)	Total cutin (ug/cm²)
1	69.3	531.4	39.6	4.4	13.2	140.4	602.2
2	73.8	430.3	28.5	3.4	11.3	142.0	861.4
3	78.6	325.5	20.1	1.5	12.5	66.1	1146.1
4	81.6	471.8	28.7	2.7	8.1	155.6	940.0
5	92.2	662.7	41.0	1.4	14.8	239.4	706.6
6	95.1	509.4	40.7	0.0	13.0	196.2	
7	103.3	456.2	44.8	1.6	10.5	196.9	717.5
8	103.4	315.4	31.0	0.0	4.9	248.6	
9	104.9	306.2	28.7	0.0	2.7	191.3	
10	110.5	418.1	39.6	0.0	7.4	189.8	1016.1
11	145.9	839.9	57.0	0.0	4.6	530.1	
r		0.5	*0.7	**0.8	*0.6	**0.9	0.2

\* Probability ≥ 0.05

\*\* Probability ≥ 0.01

Significant correlations were found between fruit water loss and content of terpenoids and sterols, and the wax components: alkanols, alkenols and iso-alkanes. Higher Alkane content in low FrWL plants may contribute to a more closely packed and less permeable cuticle.

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